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PATHOGENS AND PREDATORS OF TICKS AND THEIR POTENTIAL IN BIOLOGICAL CONTROL

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ABSTRACT

This review summarizes the literature about pathogens and predators of ticks and their potential use as biocontrol agents published since the beginning of this century. In nature, many bacteria, fungi, spiders, ants, beetles, rodents, birds, and other living things contribute significantly toward limiting tick populations, as do, for instance, the grooming activities of hosts. Experiments with the most promising potential tick biocontrol agents—especially fungi of the genera *Beauveria* and *Metarhizium* and nematodes in the families Steinernematidae and Heterorhabditidae, as well as oxpeckers—are described.

This review is dedicated to the late Prof. David Rosen (1936–1997), who was one of the major experts in the field of biocontrol of plant pests. He implanted in me a deep interest in biocontrol, encouraged me to write this review, and promised to be its coauthor. To our deep regret, his failing health prevented his participation. (MS)

INTRODUCTION

Ticks, obligatory bloodsucking arthropods, are probably the most harmful ectoparasites of domestic and wild animals as well as important vectors of disease agents to humans. Numerous pathogens and predators of ticks have been known

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for decades, but few biocontrol programs have been developed for ticks. They are controlled almost exclusively by chemical acaricides. The development of tick resistance to acaricides and our awareness that chemicals are harmful to the environment necessitate alternative control strategies such as habitat modification, use of pheromones and hormones, improvement of host resistance, and biological control. Research on the potential use of pathogens, parasitoids, or predators for the biological control of ticks lags far behind that for plant pests. The only book on the subject devotes less than one page to tick control (175).

Among the discouraging remarks are statements that natural enemies are not efficient for tick biocontrol because the population of ticks is so large and that "there is little potential for biological control (44) because the fecundities of parasites and predators appear to be far below the level required to respond to the explosive increase in tick numbers which follow certain types of weather" (197). Such statements may explain partly the longtime neglect of this field. Similar arguments were also expressed during the first steps of plant pest biocontrol.

Ticks (as well as their enemies) are most successful in their specific ecological niche. Therefore biocontrol agents may require tailor-made agents for each area, tick species, etc, in contrast to the more general effect of chemical acaricides. The first important attempt to control ticks with natural enemies started in the late 1920s, when the parasitic wasp *Ixodiphagus hookeri* was transferred from central Europe to both Russia and the United States. Several reviews describe various aspects of tick biocontrol (11, 44, 99, 106, 108, 116, 119, 139, 142, 174, 191, 199, 203, 213).

This review summarizes the major publications on tick pathogens and predators from the beginning of the century, many from publications with limited distribution, and evaluates their importance and potential use. Because of space limitations, discussion about parasitic wasps of ticks is not included.

PATHOGENS

Most pathogens enter arthropods via contaminated food. This means of entry is, however, not efficient for introducing pathogens into sucking arthropods such as ticks. Even so, some entomopathogenic fungi, as well as nematodes, can penetrate the host via the integument. How often pathogens pass from the skin of vertebrates into the alimentary canal of ticks is not known. Most pathogens are effective against arthropods only at relatively high humidities. The natural habitat of ticks—e.g. on skin or in the fur of hosts or on the ground under leaves in tropical or irrigated areas—often meets the humidity requirement of the pathogens. Several of the entomogenous microorganisms used successfully and economically against insect pests were not tested against ticks. The efficiency of pathogens depends to a large extent on the arthropod density. However, when an area is artificially overflooded with a pathogen, it may reduce a pest population nearly to zero.

Viruses and Virus-Like Particles

A high epizootic infection was described in a laboratory colony of *Alveonasus lahorensis* ticks. It caused an erosion of the tick cuticle, probably due to disorders during the molting period (189).

Virus-like particles caused damage to ticks, e.g. to the salivary gland and the synganglion. The identification of these particles is not yet clear (129, 170). *Ixodes persulcatus* females infected with a tick-borne encephalitis virus moved farther and more quickly, and were more active, than noninfected ticks (3). Viruses either do not play an important role in reducing tick populations or else knowledge is too limited to determine their effect.

Bacteria

RICKETTSIAE Most known species of rickettsiae are parasites of warm-blooded animals, but some of them also parasitize arthropods (63, 101). Ticks become adapted as vectors, reservoirs, and/or propagation sites of *Rickettsia* (168) and often harbor generalized asymptomatic infections. Rickettsial infection may lead to alterations in tick behavior, interfere with their development, and cause pathological changes in salivary glands and in ovarial tissue. In severe cases, this infection may lead to death, depending on the degree of infection, the rapidity of generalized infection, the frequency of transovarial transmission, and other circumstances (10, 91, 188). An infection with *Rickettsia prowazeki* was fatal to *Dermacentor andersoni, Dermacentor marginatus,* and *Dermacentor reticulatus* ticks but had no effect on *Hyalomma dromedarii* or *Hyalomma anatolicum excavatum* ticks (31, 166).

RICKETTSIA-LIKE ORGANISMS Rickettsia-like organisms are obligatory intracellular organisms confined in most cases to the Malpighian tubules and ovaries of their host. They exist in almost all tick species and in general are nonpathogenic (146). They are considered tick symbiotes. Rickettsia-like organisms, however, observed in the epithelial cells of the gut, in the gut content, and in the haemolymph of *Rhipicephalus bursa* female ticks caused up to 50% mortality of engorged females (71). Those from the ovarial tissues of *D. andersoni* cultivated in chicken embryos and subsequently inoculated intracoelomically into adult *D. andersoni* caused a massive, lethal infection (30).

OTHER BACTERIA The abundant bacterial flora in and on ticks is connected with their long life cycle on the ground. A wide spectrum of benign as well as fatal bacteria has been found within ticks (2, 4, 65, 68, 94, 95, 100, 115, 142, 165, 193). On host, ticks ingest bacteria with the blood of their hosts or become contaminated from their skin. Only 1.6% of unfed adult ticks and 9% of recently fed ticks contained bacteria (193). High humidity and an elevated temperature increased bacterial contamination. Latent bacterial infection may become acute and cause death when the ticks are under physiological stress, e.g. at very high humidity. Ticks infected with pathogenic bacteria turn black and die within a few days (27). Ixodid and Argasid ticks serving as vectors of *Borrelia* may be affected by the bacteria (118, 202).

Of the many pathogenic bacteria, none are specific to ticks. Some are also pathogenic to useful insects, men, and domestic animals, but they do not usually share the same ecological niche. For example, *Proteus mirabilis* bacteria might hold promise for biological control because they kill adult ticks and also cause abnormalities or mortality in the next generation (27). Also, the enterobacterium *Cedecea lapagei* was found in Brazil to infest *Boophilus microplus* via genital openings and prevent egg laying. Immersing females in *C. lapagei* suspension caused 95–100% tick mortality. The Brazilian authors expect this agent to become a promising anti-tick bioagent (28). Feeding *Ornithodoros erraticus* with *Bacillus thuringiensis* spores in blood via membrane resulted in 100% mortality. However, injecting such spores into hamsters did not influence the ticks feeding on the rodents (A Estrada-Pena, personal comunication).

Protozoa

HAEMOGREGARINA *Haemogregarina mauritanica*, a parasite of tortoises, is pathogenic to its tick vector *Haemogregarina syriacum*. Infected ticks did not feed properly and over 50% died (29).

NOSEMA *Nosema ixodis*, *Nosema parkeri*, and *Nosema slovaca* were described in ticks but only the latter was pathogenic to them. *N. ixodis* was found in adult *Ixodes ricinus*, *D. reticulatus*, and *D. marginatus* (113, 169, 171, 208). In nature, *Nosema* infections are rare but massive. The ticks stop feeding and die while still attached to the host (J Rehacek, unpublished data). Spores of *N. slovaca* inoculated into semi-engorged female ticks killed them within 14 days. More details on the *Nosema*-Ixodoidea interaction are needed to evaluate their potential use for tick control.

BABESIA *Boophilus* ticks highly infected with *Babesia bigemina* or *Babesia bovis* may have a shorter duration of oviposition, up to 98% mortality of infected females, up to 60% decreased egg production, a shorter egg incubation period, a reduced egg hatch, and a shorter larva survival. But low levels of parasitemia in the field did not kill the ticks (52, 57, 72, 155). Introducing attenuated *B. bovis* parasites to cattle also reduced their pathogenicity to *B. microplus* but did not affect infectivity (52).

THEILERIA Massive infections of the salivary glands of a superinfected *H. anatolicum excavatum* strain or *Rhipicephalus appendiculatus* with *Theileria annulata* or eleand *Theileria*, resulting in high mortality during tick engorgement and reduced reproductivity (184).

Fungi

Fungi are reported to be major pathogens of ticks because of their wide dispersal, their wide spectrum of hosts, and their ability to enter via the cuticle. Comparing egg production of *I. ricinus* females and the viability of their eggs in different habitats indicated that in a forest biotope, tick populations are low because of the presence of fungi (97). Studies in Europe (6, 41, 111, 180) indicate that fungal infection may cause the death of up to 50% of *Dermacentor*, *Ixodes*, and other ticks. However, representatives from only 6 genera out of the 57 major entomopathogenic fungi (Eumycota, Deuteromycotina) are known to attack ticks (198). In nature, 11 species of *Aspergillus*, 3 species of *Beauveria*, 3 species of *Fusarium*, 1 species of *Paecilomyces*, and 3 species of *Verticillium* are associated with ticks. Many fungi not listed as major entomopathogenic fungi were also isolated from ticks. *Metarhizium anisopliae* was not isolated from naturally infested ticks.

Entomopathogenic fungi require high humidity for germination. At low temperatures and low humidity they may parasitize the tick via the anus, and the fungus-hyphae invade the tick via the genital pore. When the relative humidity is near saturation, the *Aspergillus ochraceus* fungus may sporulate on the surface of ticks (64). Symptoms of tick fungal infection were reported frequently (11, 23, 39, 64, 97, 143).

The most commonly investigated entomopathogenic fungi are *Metarhizium* and *Beauveria* (Deuteromycotina). They are used against terrestrial insects (85) because of their wide geographic spread and host range as well as their exceptional ability to germinate even at a relatively low humidity. Various species of ticks were treated with *M. anisopliae* or *Beauveria bassiana* with satisfactory results (11, 40). Dipping *B. microplus* eggs in 1×10^8 conidia of either fungi per ml or dipping engorged females in 2.7×10^8 *M. anisopliae* caused 96–100% mortality (11, 21, 22, 40, 67, 77, 214). Spraying cattle or rabbit ears with *B. bassiana* or *M. anisopliae* showed interesting results (47, 83). Spraying earbags of cattle infested with *R. appendiculatus* ticks with 1×10^{10} *B. bassiana* or *M. anisopliae* conidia/ear, for example, caused 76% and 85% mortality and a reduction of 48% and 17.5% in egg hatchability, respectively (48, 109). *M. anisopliae* seems superior to *B. bassiana*, causing upto 96% tick mortality (11, 40, 143). Fungi can remain active on cattle ears for 1–3 weeks (109). The effect of other entomopathogenic fungi species has not yet been tested on ticks.

Ticks are affected by fungal mycelia as well as by their mycotoxins. Tetranactin-liuyangmycin (100 ppm) killed 98% of *Hyalomma detritum* larvae (84). However, application of extracts from 158 fungal strains from 29 genera on engorged female *B. microplus* ticks demonstrated that only *Aspergillus niger* extracts prevented them from laying eggs (45).

Nematodes

MERMITHIDAE Among adult *I. ricinus* ticks collected in Denmark, 6% were infected with mermithid nematodes. Up to three juvenile nematodes, 20 mm in length, were recorded per tick (120, 121). Their exact taxonomic status is not known. Their fatal effect on their hosts is primarily due to a large hole left in the cuticle when they exit the host.

HETERORHABDITIDAE AND STEINERNEMATIDAE With the success of mass cultivation, entomopathogenic nematodes have been used commercially against various insects during the last decade (122). Because their infective juveniles live in the upper layer of the soil, they are used mostly against insects living in this layer, e.g. ground-inhabiting stages of fleas (93). These nematodes have never been reported to parasitize ticks in nature. However, in 1990 it was demonstrated that they efficiently kill engorged *Boophilus annulatus* females in petri dishes (177). Engorged females of numerous other tick species were also killed by these nematodes (62, 112, 125, 179, 215). Preimaginal tick stages are, in general, the most resistant, unfed adults are somewhat susceptible, and engorged females are the most susceptible to nematodes. When nematodes are applied on a tick-infested mammal, they kill the ticks only if the mammalian skin is kept moist (112, 125, 179, 215).

The 50% lethal concentration values obtained with engorged *B. annulatus* are similar to those achieved with nematode preparations against insects (178; M Samish, E Alekseev, I Glazer, unpublished data).

The nematodes did not multiply within tick cadavers (76, 112, 215). The *Steinernema carpocasae* 'All' strain was active against *Ixodes scapularis* at 20°–30°C but less effective at 15°C, whereas the *S. carpocasae* 'DT' subpopulation of the same strain was efficient against *B. annulatus* between 14°–30°C (178, 215). Soil-filled buckets with more silt, more manure, or less moisture reduced the virulence of the nematodes (176). The anti-tick virulence and the resistance of many nematode isolates to external factors varies considerably (112, 125; M Samish E Alekseev, I Glazer, unpublished data).

There are several major reasons why nematodes may become a successful tool against ticks. First, many ticks that drop off the host tend to be highly susceptible to nematodes. Second, most engorged ticks hide for days in dark, humid upper layers of the soil, the natural habitat of nematode infective juveniles.

The immobile ticks attract the mobile nematodes. Finally, nematodes could be readily applied either by irrigation or by spraying from the ground or air at low cost, and they remain infective in humid soil for long periods (122). However, nematode use may be limited to defined ecological niches because of the susceptibility of nematodes to low humidity, high manure, or high silt concentration, the need for relatively high temperatures, and the difference in susceptibility of tick stages and species to nematodes.

Potential Use of Pathogens

Fungi from the genera *Beauveria* and *Metarhizium* and nematodes from the families Heterorhabditidae and Steinernematidae are used increasingly in commercial formulations against insects. Only a few field experiments to kill ticks with fungi (and none with nematodes) have been performed. Their value as commercial tick-control agents has yet to be proven, but their high genetic variability and possible alternative ways to improve their formulations can make them promising candidates for future use as commercial biocontrol agents of ticks. Several successful insect biocontrol pathogens have not been tested against ticks. Biological control of ticks with *Babesiae* or *Theileriae* is not promising because of their pathogenicity to vertebrates. If attenuated haemaprotozoans can be manipulated to be highly pathogenic only to the vector, they could be used simultaneously as anti-protozoan vaccines and against ticks. Attenuated parasites remain in the blood stream of the host for a long time so that they may become valuable as anti-tick agents.

PREDATORS

The efficiency of predators in controlling tick populations in different habitats varies and may reach up to 100% (67, 131, 210, 211). In Kenya, predation was lower in tall grass areas than in short grass areas (144). In Texas, predation was two to eight times higher in open areas than in a post-oak thicket pasture habitat (67). In Russia, up to 100% of the ticks were preyed on in a woody area, whereas about half were in small open areas and none in intensive pasture or agricultural areas (114).

Arthropods

TICK CANNIBALISM (ACARINA) Cannibalism of engorged females by males is reported mainly for argasid ticks (18, 66, 70, 154). In ixodid ticks this phenomenon is less common (132, 147). All unfed stages may parasitize engorged nymphs or females. Cannibalism is often found during overcrowding on a host, in laboratory colonies, or when there is a lack of host animals. This behavior leaves typical scars in the integument. The mouthparts of *Ixodes* males are functional only for copulation, and therefore they obtain most of their nutrients from engorged female ticks (147, 152). When female *Ornithodoros erraticus* were hyperparasitized by females 80% died, and when parasitized by males 30% died and egg production was reduced (92).

SPIDERS (ARANEIDA) Nine genera of spiders from six families were reported to prey on five hard tick and two soft tick genera (8, 19, 38, 43, 59, 114, 138, 144, 183, 192, 203, 211). *Teutana triangulosa* spiders prefer *Rhipicephalus sanguineus* to flies. In a garden heavily infested with *R. sanguineus*, the webs contained only tick cadavers (183). The *Schizocosa ocreata* spider killed seven times more unfed females of *Ixodes scapularis* than of *Amblyomma variegatum*, perhaps because the latter have a defensive secretion (38). Wolf spiders consumed various *I. scapularis* and *I. persulcatus* (38, 114). Eggs and engorged females were also killed by spiders (183, 211). The *T. triangulosa* spider population increased when the *R. sanguineus* tick population decreased (183). The dens of *Dysdera murphyi* are often filled with tick remains and *D. murphyi* seem to control *Ornithodoros amblus* ticks in the Guano islands of Peru (43, 141). Lavalle (117) suggested introducing spiders into bird breeding areas so as to create favorable spider microhabitats in order to control ticks in the Guano islands.

MITES (ACARINA) In laboratory trials in Australia, the mite *Anystis baccarum* preyed on an average of 38% of *B. microplus* and 69% of *Ixodes holocyclus* larvae, whereas *Anystis jabanica* preyed on only 8% of *B. microplus* larvae. *Anystis salicinus* killed 2 out of 10 *I. holocyclus* larvae but none of *Haemaphysalis longicornis*. The mites *Chaussieria warregense* and *Walzia australica* showed no interest in *B. microplus* (96). Tyroglyphid mites destroyed eggs of *I. ricinus* and *Rhipicephalus evertsi* in damp locations (164, 199). In the United States, larvae of chigger mites (*Parasecia gurneyi*) parasitized *I. scapularis* larvae feeding on lizards (154). The limited information on mites as predators of ticks is regrettable because mites are known to prey on a large variety of hosts and are used commercially to control various arthropod pests.

BUGS (HEMIPTERA) *Reduvius personatus* seemed to reduce *Alveonasus lahorensis* and *H. anatolicum* populations in the field and attacked *Alectorobius coniceps* as well as unfed *H. anatolicum* and *R. bursa* (124, 138, 209). In Angola *Phonergates bicolor* (Reduviidae) preyed on *Ornithodoros moubata* ticks. Shells of *A. coniceps* were found in hiding places of *R. personatus*, and Reduviidae were found in rodent borrows infested with *Hyalomma* ticks (138, 205).

MOTHS (LEPIDOPTERA) Larvae of the cloth moth *Tineola biselliella* devoured eggs and larvae of *O. moubata* and *Argas persicus* (207). Under laboratory conditions, 10 moth larvae each consumed an average of 23 larvae and

2.8 eggs of *O. moubata* ticks. When moths were offered wool together with ticks, they consumed both. Unidentified lepidoptera attacked ticks in the laboratory in Guadeloupe (13).

FLIES (DIPTERA) *Megaselia rufipes* and *Megaselia scalaris* flies (Phoridae) infested *Amblyomma*, *Anocentor*, *Boophilus*, and *Ixodes* ticks mainly as saprophytic pests in laboratory colonies (9, 75, 153, 203; M Samish, E Alekseev, unpublished data). *Megaselia* larvae emerged from the ticks and infested their eggs. In Zimbabwe, Phoridae flies infested *Boophilus decolorotus* and *B. microplus* female ticks, which produced half as many eggs as the fly-free control group. Apparently *Asilid* flies also attack ticks (186, 199). Up to 25% of *I. scapularis* engorged females collected in Russia were infested by *M. rufipes* (9). Whether the flies infested only dead or also live ticks is still an open question.

ANTS (HYMENOPTERA) Some 27 species of ants from 16 genera, mainly *Aphaenogaster*, *Iridomyrmex*, *Monomorium*, *Pheidole*, and *Solenopsis*, are known to be tick predators. Ants are known to prey on most tick genera. *Monomorium minutum* (*Monomorium pharaonis*) and *Solenopsis saevissima* fed on tick eggs (86, 98, 106, 199, 203) but *Aphaenogaster longiceps*, *Chalcoponera metallica*, *Iridoxyrmex detectus*, and *Notoncus foreli* did not. Preying on eggs by *Pheidole megacephala* and *Solenopsis invicta* ants is controversial (40, 56, 67, 86, 211). The eating preferences of ant species differ, some preferring larvae and others preferring engorged or unfed adults (13, 54, 56, 142, 157, 211). The time of day, brightness, and air humidity influenced the anti-tick activity of ants (203).

Ants are thought to be important tick killers of *A. miniatus*, *B. annulatus*, *B. microplus*, *Otobius megnini*, and *Otobius moubata* (12, 19, 20, 51, 98, 157). Duffy (60) found a negative correlation between ant and tick populations in nesting seabird areas and assumes this is due to predatory ants. In Mexico, *Solenopsis geminata* consumed 63–100% of engorged *B. microplus* females (35) and in Guadeloupe, 7–18% of engorged stages of *A. variegatum* (13). Introducing *S. invicta* into the United States markedly reduced the number of anaplasmosis seropositive cattle in Louisiana (105, 204). An invasion of *S. invicta* reduced the *Amblyomma americanum* population from 56 to 0.3 ticks/unit area (32). Controlling *Solenopsis richteri* ants with Merix ant bait dramatically increased the survival of *A. americanum* eggs and engorged larvae. Three months after engorged ticks were introduced to an ant-infested area, the untreated plot contained only 12% of the ticks recovered from the anti-ant–baited plot (86).

In Australia no correlation was found between the density and distribution of 136 ant species and the numbers of *Amblyomma limbatum* or *Apo. hydrosauri* ticks (42). *P. megacephala* are known to prey on ticks. About 1300 ants consumed 220 engorged *B. microplus* females daily (56, 58). The type of vegetation affected the anti-tick activity of ants. The predation in open areas was two to eight times higher than in woody ones (67, 144). In the laboratory, *Rhytidoponera* sp. ants preyed on *Ixodes purpureus* ticks on bare soil more than on soil covered with leaf litter (54). Wild rabbits living in *Formica polyctena*–infested plots had far fewer ticks than those in ant-free plots, and rabbits sprayed with formic acid were free of ticks for at least 5 days (36).

BEETLES (COLEOPTERA) In Russia, 17 species of beetles of 8 genera were shown to have trophic relations with hard ticks (24, 158, 206). Carabid, Cantharid (*Chauliognathus pennsilvanicus*), and Silphid (*Ablattaria laevigata*) beetles were seen to feed on ticks (37, 74; E Alekseev, M Samish, unpublished data).

Beetles preyed mainly on engorged ticks whereas eggs and unfed larvae were rarely attacked (24, 37, 114, 131). One Carabid or Cantharid beetle consumed one to five ticks within 1–2 days (37, 158). Dermestid beetles in bat guano fed on engorged Argasid ticks that had fallen into the guano (138).

Of eight ground beetle species from woods in Russia, 62% were seropositive to *I. persulcatus* (24). *I. persulcatus* is active during April and beetles start to be active during May. The number of beetles decreases in July, parallel to the reduction in tick population (24). Any interaction between the two populations, however, is only speculative.

OTHER ARTHROPODS A single Forficulidae representative preyed on approximately 1800 *B. microplus* eggs in 10–12 days (203). Red rock crabs (*Grapsus grapsus*) in the Galapagos picked off ticks (probably *Amblyomma darwini*) from marine iguanas (*Amblyrhynchus cristatus*) (159). Miriapoda or *Phalangium opilio* (Phalangida) consumed unfed larvae or nymphs of *I. persulcatus* in dishes (114).

Amphibians

TOADS Toads ingested ticks in the United States (199) and in Brazil (*Bufo paracnemis*) (73, 203). Engorged female ticks were used successfully as bait for *B. paracnemis*, which readily consumed preimaginal and adult ticks (73).

TORTOISES The water-tortoise *Pelomedusa subrufa* was observed to remove ticks from black rhinos in a streambed (142).

Reptilians

Ticks are only rarely mentioned as lizard food even though some lizards eat mainly arthropods. The Iguanid lizard (*Tropidurus* sp.) was probably introduced into the Guano islands for the control of bird ticks (43). The lizards' stomachs contained 2.4–15 ticks/stomach (probably *O. amblus*) (59). However, because there are few lizards near the bird nests, their effect on the tick population is limited (59). Several other lizard species were also found to be inefficient tick predators (8, 126, 127, 142, 148, 150).

Avians

Birds are generally thought to be the main predators of ticks. This impression is based mainly on sporadic observations, except for oxpeckers. Birds either perch on tick-infested mammals (21 bird species), pick the ticks off the host during flight (1 species), or collect them from the ground (9 species). Only 14 species of birds were shown to have ticks in their crops or gizzards. Oxpeckers are the only birds that specialize in feeding on ticks, but many other bird species consume them eagerly. For example, young *Pica pica* birds that had never encountered ticks preferred a diet of ticks when offered a choice (182).

OXPECKERS The family Buphagidae includes two species. The yellow-billed oxpecker (YBO), *Buphagus africanus*, is found from Senegal to Ethiopia in the East and in Natal in the South, whereas the red-billed oxpecker (RBO), *Buphagus erythrorhynchus*, lives primarily on the eastern side of the African continent. Their regions overlap (33).

The RBO devotes some 94% of its feeding time to scissoring based on touch rather than sight, ingesting mainly hair and small arthropods, and it also plucks pieces of skin. It may peck sores or catch insects in the air (7, 17, 195).

The daily food of mature oxpeckers averaged about 13,000 larvae or 100 engorged *Boophilus decoloratus* female ticks/bird, as established by counting their stomach contents (195). The maximum number of engorged *Amblyomma hebraeum* larvae consumed by a young RBO within 24 h was 7195, weighing 14.2 g (17). In 1933, Moreau calculated that Tanzania (Tanganyka) had about one RBO per three head of cattle (137). RBOs feeding on cattle infested with engorged female and male ticks consumed the female ticks first (195). When cattle with larvae, nymphs, or adult *B. microplus* were kept separately, two young RBOs per fly cage ingested within 1 week 53% (1176 larvae), 9% (1549 nymphs), or 95% (1293 adults) of the ticks on each host (17).

The abundance of tick species in the area did not correlate with those found in the bird's stomachs. For RBOs in captivity, with ticks on cattle or in dishes, the first choice was *B. decoloratus*, the second *R. appendiculatus* and *Hyalomma truncatum* females, and the third *H. rufipes*, *R. evertsi evertsi* and *A. hebraeum* females (17, 195, 137, 201).

The RBO has a wide range of preferred ungulate hosts, including 11 species of large mammals (81). The YBO seems to prefer large ungulates with a short or sparse pelage, mainly buffalo and white rhinoceros, whereas the RBO, better adapted to scissoring, feeds mainly on long-haired animals (7, 34, 81, 137). Oxpeckers do not forage on elephants.

When RBOs forage on a mixed livestock herd, they prefer cattle and horses to sheep, pigs, or goats, and they prefer weak individuals not treated with acaricides. They feed repeatedly on specific individuals even in a homogenous herd (201). Some hosts only gradually permit contact with newly introduced birds but later even expose different parts of their bodies to the birds (protocooperation) (25, 33).

Oxpeckers may enlarge existing or healing wounds by consuming skin fragments and blood. Their ability to cause wounds on intact skins has not been proven, although most pasture animals have open or semi-healed wounds. The YBO is more aggressive and feeds more often on wounds than does the RBO (195; C Foggin, personal communication). Heavy grease of Stockholm tar on a wound deterred oxpeckers (201). RBOs were sore-feeding on various mammals for 0.4–2.8% of their time (17). Feeding on wounds may spread mammalian pathogens; however, this has not been proven (33, 137). It is agreed that the advantages of oxpeckers by far outweigh their disadvantages (17, 201).

When 47 YBOs were reintroduced into the Rods Matopos National park, they became established (79, 80). In such areas where oxpeckers have been reintroduced, fewer calves have died and the number of ticks on hunted animals has decreased markedly (50, 53, 79, 80). When 187 oxpeckers were transferred to 10 small game farms, they became established in at least four of the parks (50). RBOs have been bred successfully in the Zurich zoo (110). Conditions for the successful introduction of oxpeckers should include a suitable location to catch them while they feed on tame animals. The new location should be of at least 3000 ha with 500 or more game animals or domestic animals. A favorable climate for the birds and a monitoring technique for the tick population are needed. The birds must be released at least 10 km from an anti-tick dipping area. Groups of at least 20 birds should be translocated, and prevention of panic among the hosts during their first contact with oxpeckers is important (50, 140).

The RBOs are less aggressive and less host-specific than the YBOs and live in marginal areas. Thus they have a better chance to become established (7, 34, 50, 82, 96, 195).

The density of oxpecker populations depends largely on the amount of available ticks, but the tick population may still remain high (149). Ticks on game animals can support a high bird population for the benefit of domestic animals (123).

CATTLE EGRETS *Bubulcus ibis (Ardeola ibis)* tend to forage near and on large animals. This led to the assumption that ticks are an important part of their diet (160, 185, 190). It was therefore suggested that egrets be introduced into New Zealand for the control of *Haemaphysalis bispinosa* ticks (145). However, the average number of ticks found in Florida, South Africa, Guadeloupe, and Australia was only one to five ticks per egret. In Brazil and the Middle East, there was an average of 33–68 ticks per egret (13, 14, 26, 69, 107, 128, 161, 203). Of the ticks ingested, 20% were either lacking or had cement cones around their hypostom (128). This suggests that the birds picked at least part of the ticks off their hosts. Egrets picked more ticks from the grass than from cattle (199). Nearly all ticks found in egrets were engorged females (13, 14, 128).

The ticks identified within cattle egrets were *A. variegatum*, *Boophilus australis*, *B. decoloratus*, *B. microplus*, *Hyalomma aegyptium*, and *Rhipicephalus* sp. (13, 14, 128, 199). In most parts of the world, cattle egrets seem to have little influence on the size of a tick population, but Verissimo (203) estimates that in Brazil the tick population was reduced by up to 66%.

DOMESTIC FOWL The omnivorous *Gallus domesticus* often pick ticks from the ground and remove attached ticks from domestic animals (16, 20, 61, 89, 90, 102, 131, 151, 199). Hungry chickens in Kenya that were confined to an area of 42 m^2 with 10 resting cattle (89, 90) collected 74–81 ticks per h/bird, and two chickens consumed 229 ticks within 3 h. Chickens seem to prefer *R. appendiculatus*, which concentrate close to the ears and eyes of cattle (89, 90, 167). At a high density of ticks, an average of 69% of the ticks were consumed, but at a low density only one tick was consumed per bird (13, 89, 90). Helmeted guinea fowl (*Numida meleagris*), known to consume a wide variety of arthropods, reduced an unfed adult *Ixodes dammini* population significantly (61).

OTHER BIRDS In addition to oxpeckers, cattle egrets, and domestic fowl, some 43 other bird species also feed on ticks. Among these, some 29 species belong to the large order of songbirds (Passeriformes) and some 1–4 species each belong to six other orders (Charadriiformes, Ciconiformes, Coraciformes, Cuculiformes, Galliformes, and Tinammiformes). The value of birds as suppressors of tick populations in nature is difficult to evaluate. It appears that the motionless engorged ticks are an easy and tasty prey to many birds, which thus helps to reduce the tick population. Ravens ate between 1–29 ticks/bird (162) and 24 *Pica pica* birds consumed 5% of 1400 female ticks (182). Verissimo (203) reports that the alimentary canal of a small falcon in Brazil was filled only with ticks. In South Africa, however, only 36 ticks were recovered from 7334 birds comprising 239 species (exclusive of oxpeckers), indicating their low importance as tick killers (161). The results of experiments on the importance of birds in suppressing tick populations vary considerably for different countries, seasons, types of ground cover, etc (1, 131, 144, 161, 162). In an open area, 43% or 91% of the ticks disappeared, but under a bird-proof screen only 6.4% or 27% disappeared (131, 144).

Tick hosts often stand still or even uncover hidden skin areas to the birds to support deticking, e.g. moose with ravens, black-tailed deer with cow's scrub jays, bushbucks with Indian mynahs, and marine iguana with Galapagos finches (5, 103, 156, 162, 182, 194). This cooperation indicates a long history of protocooperation.

Gray jays and ravens visited pens with tick-infested moose 30 times, whereas none visited noninfested moose pens. Gray jays and magpies picked up all of the ticks first from either a bread-tick or an animal hair-tick mixture (1, 182). Scrub jays were observed to spend 89% of their time searching deer for ectoparasites (103). Ravens will also pick ticks from drying animal skins (162). Ravens and gray jays often store live ticks (1, 182), thus helping to rescue ticks from acaricide-treated areas and to distribute them.

Only one tick species was usually found within a bird, but at times up to eight tick species have been reported within one bird (5, 162).

Mammals

SHREWS (INSECTIVORA) The shrews *Crocidura hirta(?)*, *Crocidura nigrofusca*, and *Sorex araneus* preyed on ticks and at times preferred them to alternative food (131, 144, 187). Shrews seem to locate hidden ticks by their smell. Milne (131) regards shrews as highly important in the control of preovipositing ticks.

RODENTS Mice and rats are often cited as preying on ticks, but the evidence is mostly circumstantial. Several species have been observed to attack engorged ticks (144, 210). Some rodents did not touch ticks in the laboratory (131, 187), and *Microtus arvalis*, *Mus musculus*, and *Herpestes auropunctatus* had barely any interest in ticks in the field (13, 163). In the laboratory, *Sigmodon hispidus* and *M. arvalis* (mice or rats) ate ticks avidly (46, 163, 199, 212; E Alekseev, M Samish, unpublished data). *Peromyscus leucopus* mice ate some 50% of unfed *I. scapularis* nymphs, which tried to feed on the mice but were consumed before they were able to attach (200).

Rodents consumed engorged ticks before they could hide but were less successful with the mobile unfed stages (12, 98).

Small mammals eliminated *A. americanum* engorged females far more efficiently in a post-oak thicket habitat than in open pastures (67). According to Sergent et al (185), *Hyalomma mauritanicum* spends its diapause in cracks of walls where they cannot be reached by mice. Hispid cotton rats consumed ticks only in fields with little greenery (46). In South Africa, the stomach contents of 1640 small- and medium-sized mammals from 23 families were checked for ticks; a total of 6 ticks were found, only in caracals (3.5%). This demonstrates the minor importance of such mammals as tick predators in this region (112a).

Other Vertebrates

The amount of ticks ingested by grazing herbivores has not been studied but it may be high. The weaker animals in a population of mammals tend to have a greater tick burden, and they also represent a larger proportion of the prey of carnivores. This may cause a greater-than-expected reduction in total tick population (149).

Self-licking (grooming) is one of the most common parasite defense behaviors of vertebrates. Rodents, felines, ruminants, and primates are known to groom. Cats have far fewer ticks than dogs, probably because of their superior grooming habit. Rats spent one third of their waking time grooming, and antelopes groomed 600–2000 times within 12 h (87). Restraining cattle increased the *B. microplus* tick population four times, and restraining impala increased the number of ticks 20 times (15, 136). When the dental comb on Impala was closed with cement, their tick population increased eight times (87). A higher tick infestation increased grooming activity and spraying with acaricides reduced it (136, 181).

Tick-resistant mammals groom more often, and if they are restrained, their tick population tends to rise more than on restrained susceptible hosts (15, 173). Grooming activity increases in seasons and areas with a large number of questing ticks (88, 133, 181). The sex of a host and its breeding status also influenced grooming activity (134, 135).

Grooming of cattle seems to be most effective against *B. microplus* during the first 24 h post-larva infestation (15). Moose infested by *Dermacentor albipictus* groomed mainly during the engorgement of nymphs and adult ticks (181).

Potential Use of Predators

Predators contribute greatly to a reduction in the tick population. Because none of them (except oxpeckers) are tick specific, their importation is generally not recommended. Local predators should, however, be conserved and augmented.

Insecticides also suppress arthropods that prey on ticks. Thus, using less insecticide that is more specific to the target, and minimizing the area of its distribution to tick-infested areas, would contribute to the preservation of these predators.

Spiders have defined habitats. A change in the habitat, such as mulching, may increase the spider population by as much as 60% (104, 172). Native ant species could be manipulated so as to assist in the control of ticks (49, 78).

Conservation of a bird population (for example by providing nesting sites, supplying drinking water, and avoiding the use of dangerous chemicals) may contribute to a reduction in tick populations.

Mixed husbandry farms heavily infested with ticks could be advised to keep birds together with their cattle, as is often done in Kenya, Sudan, and India (90, 130), even though their effect on the number of ticks seems to be limited.

During the last few decades, RBOs nearly disappeared in certain areas because of a decrease in game animals (and their ticks) and the introduction of bird-poisoning acaricides (33, 50, 79, 201). However, they are gradually returning to those areas that use safer acaricides (e.g. amitraz, pyrethroids) and where the population of game animals has increased and RBOs have either returned naturally or been reintroducted. Because oxpeckers may at times also be harmful (as discussed above), their introduction into a new area should be weighed carefully.

Additional information on the physiological and genetic basis for signaling the need to groom could help to foster this advantageous behavior.

CONCLUDING REMARKS

It is estimated that to date only about 15% of existing natural enemies of insects have been discovered. Yet for some insect species, over 100 enemies are known (55). Even less information exists about tick enemies than about insect enemies.

The life cycle of ticks is primarily spent away from their hosts, where they may be killed by various pathogens or enemies. The enemies attacking ticks on their hosts (e.g. parasitic wasps, oxpeckers) are usually more specialized, and they are also more efficient when the tick concentration is high.

Many pathogens and predators of ticks are listed in this review. We hope it will encourage scientists and policy makers to turn this neglected, important field into an active branch of research and develop it as a component of integrated tick management. However, as yet only a few experimental data exist on the impact of tick enemies under field conditions. Such studies are essential for the development of an effective tick biocontrol program.

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